
Conservation Priorities for Chukar Partridge in Israel Based on Genetic Diversity across an Ecological Gradient

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Abstract: *Recent studies suggest that patterns of genetic diversity significantly influence the viability and persistence of local populations. Revealing and mapping spatial patterns of genetic diversity within species' ranges may be vital when defining criteria and prioritizing areas for conservation. Chukar Partridges (*Alectoris chukar*) in Israel occur along a steep ecogeographical gradient extending from mesic Mediterranean zones in the north to steppe and desert regions in the south. To test the hypothesis that the most genetically diverse populations within a species' range occur within the ecotone, an area of transition between ecosystems where a sharp environmental gradient exists, we examined the allozyme diversity of chukars collected at five locations within the species' continuous range in each of 2 years. Based on 32 allozyme loci, the genetic diversity of chukars increased significantly along a gradient from populations in Mediterranean regions to those at the ecotone in the northern Negev desert, despite close geographical proximity among populations. Genetic diversity as estimated by percent polymorphic loci, observed and expected heterozygosity, and mean number of alleles was not homogeneous among sampling localities: single and multilocus Hardy-Weinberg and linkage disequilibria increased along the gradient toward the ecotone. Populations exhibited some isolation by distance effects in the face of substantial gene flow. We therefore recommend that higher conservation priority be assigned to the Mediterranean-Negev ecotone area. For Chukar Partridges, it supports the highest overall genetic diversity as well as unique alleles. Priorities for other populations, moreover, can also be set based on their genetic diversity across ecological gradients. Rapid urbanization of Israeli landscapes threatens to disrupt unique and perhaps essential genetic connections among chukar populations, and management of chukars in Israel within a metapopulation context is an urgent requirement.*

Prioridades de Conservación para *Alectoris chukar* en Israel, Basadas en la Diversidad Genética a lo Largo de un Gradiente Ecológico

Resumen: *Estudios recientes sugieren que los patrones de diversidad genética influyen significativamente la viabilidad y persistencia de poblaciones locales. La identificación y mapeo de patrones espaciales e diversidad genética intraespecífica puede ser vital cuando se definen criterios para la priorización de áreas para conservación. En Israel *Alectoris chukar* ocurre a lo largo de un gradiente eco-geográfico pronunciado que se extiende desde zonas del Mediterráneo en el norte y estepas y desiertos en el sur. Analizamos la diversidad de alozimas de *A. chukar* colectados en cinco localidades dentro del rango continuo de la especie en los años 1990 y 1993, para probar la hipótesis de que las poblaciones genéticamente más diversas dentro del rango de una especie ocurren dentro del ecotono; un área de transición entre ecosistemas donde existe un gradiente ambiental pronunciado. Sobre la base de 32 loci de alozimas, la diversidad genética de *A. chukar* se incrementó significativamente a lo largo del gradiente de las poblaciones en las regiones del Mediterráneo*

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*hacia aquéllas ubicadas al Norte en el ecotono del desierto de Negev, a pesar de la proximidad geográfica entre poblaciones. La diversidad geográfica estimada como el porcentaje de loci polimórficos, la heterocigosidad observada y esperada y el número promedio de alelos, no fueron homogéneos entre las localidades muestreadas. Los desequilibrios de enlace y de Hardy-Weinberg, sencillos y multilocus, se incrementaron a lo largo del gradiente y hacia el ecotono. Las poblaciones exhibieron cierto aislamiento por efecto de la distancia a pesar de existir un flujo génico sustancial. Recomendamos por ello, que las prioridades de conservación más altas sean asignadas al área del ecotono del Mediterráneo-Negev. Esta área contiene la mayor diversidad genética de la especie, así como alelos únicos. Las prioridades para otras poblaciones pueden también ser establecidas en base a su diversidad genética a lo largo de gradientes ecológicos. La rápida urbanización del paisaje israelí amenaza con romper las únicas y por cierto esenciales conexiones genéticas entre poblaciones de *A. chukar*. El manejo de *A. chukar* en Israel dentro de un contexto de metapoblaciones en un requerimiento urgente.*

Introduction

Recent studies in conservation genetics suggest that patterns of genetic diversity significantly influence the viability and persistence of local populations (Vrijenhoek 1994; Frankham 1996; Riddle 1996; Lacy 1997). The widespread application of molecular tools has revealed a number of examples of genetic structuring of natural populations at relatively small geographic scales (Avise 1992; Prinsloo & Robinson 1992; Randi & Alkon 1994; Nevo et al. 1997). Moreover, understanding geographic patterns of genetic diversity is highly relevant to conservation biology and especially to decision procedures allowing systematic rather than opportunistic selection of populations and areas for in situ protection (Pressey et al. 1993). Therefore, awareness of this component may be vital to defining criteria and prioritizing for conservation and wise use of genetic resources (Brooks et al. 1992).

Intraspecific genetic diversity can be generated by various evolutionary mechanisms, including (1) clinal variation of neutral (Wright 1943; Slatkin 1993) or adaptive traits (Endler 1977); (2) historical isolation of subdivided populations (Wright 1931; Slatkin 1994); and (3) secondary contacts among formerly isolated and divergent populations (e.g., hybrid zones; Barton & Hewitt 1989). In the case of newly founded or small, isolated populations, the effects of random drift may prevail over adaptive changes (Endler 1977). The interplay between the homogenizing effects of gene flow and the divergent pressure of natural selection among populations in different habitat conditions may generate different functional adaptations, increase genetic diversity, and ultimately lead to speciation (Rice & Hostert 1993).

Ecological transition zones (i.e., ecotones) may play a crucial role in generating and maintaining biodiversity (Smith et al. 1997). Divergent selection can produce morphological differentiation in the presence of high gene flow across ecotones between contiguous populations (the divergence-with-gene-flow model of speciation; Rice & Hostert 1993; Smith et al. 1997). Morpho-

logical divergence is also generated at small geographic scales in species that have great potential for dispersal and gene flow across environmental gradients (Mitchell-Olds 1992; Peterson 1995 and references therein). Accordingly, ecotones may serve as "hot spots" of genetic diversity within species' ranges and thereby may warrant high conservation priority (Smith et al. 1997).

Located at the confluence of three continents and four biomes (Mediterranean, desert, steppe, and subtropical African), Israel encompasses steep climatic and ecological gradients within a small geographical space (Kadmon & Danin 1997). A steep part of the north-south precipitation and climatic gradient in Israel is a transition belt approximately 60 km wide at the northern margins of the Negev desert. This zone represents the ecotone between Mediterranean, steppe, and desert ecosystems (Safriel et al. 1994) where a relatively sharp rainfall and floristic gradient occurs (Kadmon & Danin 1997; Fig. 1). Various plant and animal species attain their distribution edge in Israel within or near this belt (see examples from diverse taxonomic groups in Yom-Tov & Tchernov 1988).

The Chukar Partridge (*Alectoris chukar*), a Eurasian phasianid, is widely distributed in Israel. The southern Negev desert of Israel and the Sinai desert of Egypt comprise the southwestern periphery of the species' natural global range (Cramp & Simmons 1980; Randi et al. 1992). The chukar's continuous distribution in Israel extends from Mediterranean areas in the north (Galilee), with mean annual rainfall 500–1000 mm, to the desert margin of the northern Negev and the Negev highlands in the south, where mean annual rainfall is 100–200 mm and rainfall distribution is more temporally and spatially variable than in the mesic north (data from Israel Meteorological Service and Y. Morin, personal communication). The ecotone between desert and Mediterranean zones is near the margins of the chukar's continuous range in Israel. In extremely arid regions south and east of the central Negev desert, where mean annual rainfall is less than 100 mm, chukar distribution becomes patchy and sparse and is usually associated with natural sources of open

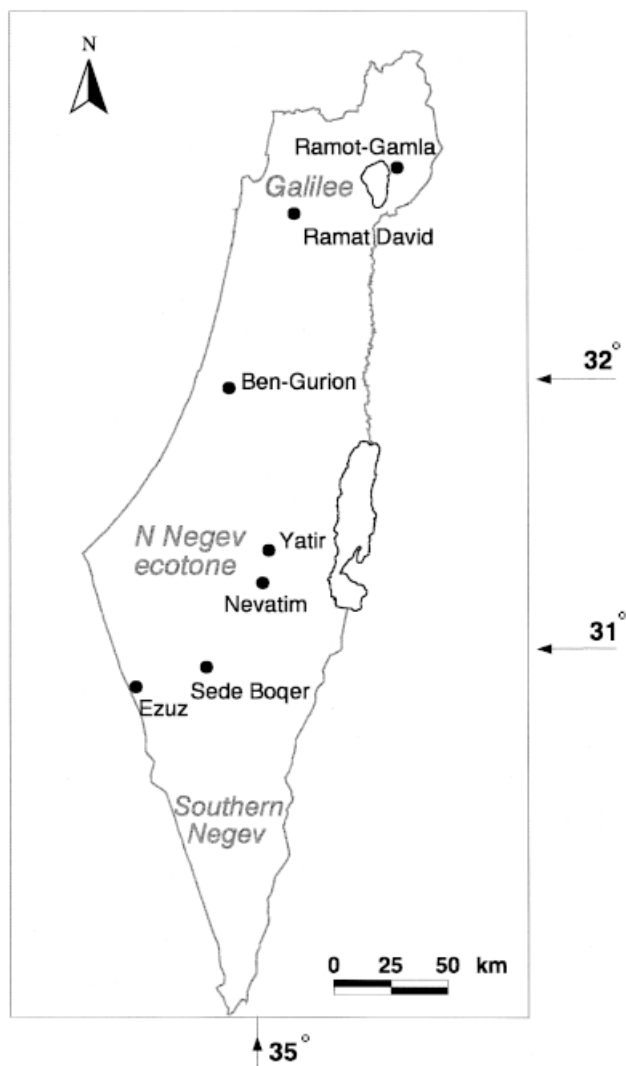


Figure 1. Map of Chukar Partridge sampling localities in Israel. Galilee, the northern Negev ecotone, and southern Negev regions are marked in italics for general orientation.

water or irrigated agriculture (Carmi-Winkler 1985; Shirihai 1996).

Previous studies suggest substantial geographic variation in morphological (Nissani 1974) and genetic traits (Randi & Alkon 1994) among chukar populations in Israel. We explored the working hypothesis that the highest genetic diversity within the species' range occurs where ecological transition zones or ecotones occur. Based on this hypothesis, diversity is expected to peak in ecotone areas and decline along a gradient moving away from this area. If this is the case, under the assumption that high genetic diversity confers high conservation priority, an increasing gradient in conservation priority should follow the ecological gradient from Mediterranean to ecotone regions and areas of environmental change

that maintain high levels of biodiversity should receive especially high priority (Smith et al. 1997). We tested this hypothesis in the Chukar Partridge in Israel.

Methods

Sample Collection and Handling

We obtained samples from Chukar Partridges in 1990 and 1993 collected at seven sites along a steep ecogeographic gradient extending from the Lower Galilee and Golan Heights in the north to the ecotone at the northern Negev and the central Negev in the south (Fig. 1). Five populations were sampled in each year of study during the nonbreeding season, when birds are organized in stable coveys that maintain relatively fixed home ranges (Alkon 1974), including three that were studied in both years (Table 1). Birds were hunted by rangers of the Israel Nature Reserves Authority and by authorized hunters, following Randi and Alkon (1994). Heart and liver tissues were dissected from birds in the field, stored in ice coolers, and transferred within several hours to laboratory freezers kept at -20° or -80° C.

Genetic Analysis

Tissue samples were homogenated separately, and clear supernatants were collected and stored at -80° C in aliquots. Polyacrylamide gel electrophoresis, staining of allozyme products, and genetic interpretation of electromorph mobility were performed following Randi and Alkon (1994). Thirty-two putative loci were resolved for each year's samples. The same loci were resolved and compared for both years, except for sME and sIDH, which were resolved for the 1990 samples only, and PEP-1 and AMY-2, which were resolved for the 1993 samples only.

The following estimates of genetic diversity were computed for each population (with BIOSYS-1, version 1.7; Swofford & Selander 1989): percent polymorphic loci (P); mean number of alleles per locus (A); mean observed heterozygosity (H_o); and mean Hardy-Weinberg and expected heterozygosity (H_e). Total genetic diversity (H_t), estimating the heterozygosity of each polymorphic locus, was computed as $H_t = 1 - \sum p_i^2$, where p_i^2 is the mean frequency of the i th allele at its locus as determined from electrophoretic analyses (Nei 1973) using DISPAN (Ota 1993). Hardy-Weinberg equilibrium was assessed by Fisher's exact test (Haldane 1954) with GENEPOP (version 1.2; Raymond & Rousset 1995). Under the null hypothesis of random union of gametes, the probability was tested in every population for each locus separately, as well as across all loci. In addition, F_{IS} , which estimates within-population deviations from random mating (following Weir & Cockerham 1984), was calculated in

Table 1. Summary description of Chukar Partridge collection sites along a north-south gradient in Israel.

Population and year of sampling*	Sample size	Habitat
Ramot-Gamal 1990 (RG90)	29	open oak park forest, chaparral; orchards and field crops
Ramat-David 1993 (RD93)	26	ruderal vegetation; field crops (airport)
Ben-Gurion Airport 1990 (BG90)	27	ruderal vegetation (airport)
Ben-Gurion Airport 1993 (BG93)	35	
Yatir 1990 (YT90)	30	herbaceous community;
Yatir 1993 (YT93)	29	pine plantation, orchards
Nevatim 1993 (NV93)	25	open semidesert vegetation; small, local, traditional orchards and vineyards
Sede Boqer 1990 (SB90)	32	desert semishrub; orchards and field crops
Sede Boqer 1993 (SB93)	34	
Ezuz 1990 (EZ90)	17	desert semishrub; field crops

*See Fig. 1 for locations.

each locus with GENEPOP. Departures from Hardy-Weinberg equilibrium produce F_{IS} values significantly less than 0 (excess of heterozygotes) or more than 0 (deficiency of heterozygotes). The significance of deviation of F_{IS} estimations from 0 was tested with GENEPOP, following Raymond and Rousset (1995).

Pairwise estimates of linkage disequilibrium (Lewontin & Kojima 1960) were calculated with LINKDIS (Black & Krafur 1985). Linkage disequilibrium was estimated as mean within-population R (Black & Krafur 1985), a correlation coefficient of pair-wise occurrence of alleles in individuals and populations, based on an unbiased estimate of composite linkage disequilibrium (Cockerham & Weir 1977) that is corrected for heterozygosity and departures from random mating (Weir 1979). The number of pairs of loci that are not in genotypic equilibrium in each population was computed by Fisher's exact test under the null hypothesis that, within a pair of loci, genotypes at one locus are independent from the genotypes at a second locus (GENEPOP). The geographic population structure was analyzed with F statistics (Wright 1965; Mills & Allendorf 1996), particularly F_{ST} , which describes deviations from random mating among individuals from different populations and the proportion of among-population genetic diversity. Values of F_{ST} significantly >0 indicate significant spatial population structuring. The value of F_{ST} (with confidence intervals) was estimated as Φ by Weir and Cockerham's (1984) approach as implemented in the computer program FSTAT (version 1.2, Goudet 1993). Significance of genotypic differentiation among populations was tested by Fisher's exact test (GENEPOP).

Gene flow among populations (i.e., the product of effective population size and migration rate) was estimated as $Nm = (1 - F_{ST})/4F_{ST} = 1/4(1/F_{ST} - 1)$, assuming an island model at equilibrium (Wright 1965; Slatkin 1993). Alternatively, Nm was estimated by means of the frequency distributions of private alleles (Slatkin & Barton 1989). Isolation by distance was tested following Slatkin (1993). Pairwise estimates of gene flow among populations were computed as $\hat{M} = (1/F_{ST} - 1)/4$, and isolation by distance was

assessed from the regression $\log_{10}(\hat{M}) = a + b \log_{10}(\text{geographical distance in km})$ with the program DIST (Slatkin 1993). In cases of isolation by distance, the relationship among $\log_{10}(\hat{M})$ and $\log(\text{km})$ should be linear, and b should be significantly negative (Slatkin 1993). The significance of correlation among gene flow and distances was assessed by the Mantel test (Mantel 1967), as implemented in GENEPOP.

Correlation Calculations

To test for trends in within-population diversity along the gradient, for each year we ranked the five populations on an ordinal scale from 1 for the northernmost population (Ramot-Gamal in 1990 and Ramat-David in 1993) to 5 for the southernmost populations studied (Ezuz in 1990 and Sede Boger in 1993). Spearman rank correlation coefficients (Sokal & Rohlf 1981) and their two-tailed significance were computed between location ranking and each of the following population genetic diversity parameters: percentage of polymorphic loci (P), observed heterozygosity (direct count) (H_o), Hardy-Weinberg expected heterozygosity (H_e), and mean number of alleles per locus (A). They were also computed between location ranking and linkage disequilibrium levels as estimated by R . Correlation between sample size and diversity parameter values was computed. Correlations were calculated with SPSS for Windows (Norušis 1993).

Results

Trends in Diversity along the Gradient

Chukar populations were polymorphic at 16 and 14 of 32 loci in 1990 and 1993, respectively (Table 2). Thus about half of the studied loci were polymorphic, and about 30% of the polymorphic loci had H_i values over 20% (Table 3), indicating high levels of gene diversity in Israeli chukar populations (also see discussion in Randi & Alkon 1994).

Table 2. Polymorphic loci and allele frequency in populations of Chukar Partridges sampled in 1990 and 1993 in Israel.

Locus	Allele	Population*									
				BG		YT		NV 1993	SB		EZ 1990
		RG 1990	RD 1993	1990	1993	1990	1993		1990	1993	
CK	a	0.017	0.050	0.093	0.043	0.167	0.065	0.100	0.109	0.086	0.059
	b	0.983	0.950	0.907	0.957	0.833	0.935	0.900	0.891	0.914	0.941
ALB	a	1.000	1.000	1.000	1.000	0.967	1.000	1.000	1.000	0.971	1.000
	b	0.000	0.000	0.000	0.000	0.033	0.000	0.000	0.000	0.029	0.000
LDH-1	a	0.034	0.000	0.000	0.000	0.033	0.034	0.000	0.000	0.000	0.029
	b	0.966	0.100	1.000	1.000	0.967	0.966	1.000	1.000	1.000	0.971
sGOT	a	0.000	0.038	0.000	0.029	0.000	0.086	0.140	0.000	0.172	0.000
	b	0.879	0.788	0.704	0.871	0.850	0.690	0.720	0.750	0.578	0.647
	c	0.121	0.173	0.296	0.100	0.150	0.224	0.140	0.250	0.250	0.353
SOD-2	a	0.466	0.212	0.296	0.314	0.383	0.500	0.300	0.312	0.368	0.321
	b	0.534	0.788	0.704	0.686	0.617	0.500	0.700	0.688	0.632	0.676
EST-2	a	0.190	0.481	0.167	0.118	0.316	0.397	0.280	0.312	0.333	0.323
	b	0.379	0.231	0.463	0.397	0.183	0.172	0.140	0.219	0.258	0.294
	c	0.328	0.173	0.296	0.265	0.317	0.397	0.460	0.359	0.212	0.265
	d	0.017	0.096	0.000	0.221	0.017	0.000	0.020	0.047	0.015	0.059
	e	0.086	0.019	0.074	0.000	0.167	0.034	0.100	0.063	0.182	0.059
sMDH	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.984	1.000	1.000
	b	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000
6PGD	a	0.000	0.000	0.000	0.029	0.000	0.000	0.000	0.000	0.000	0.000
	b	0.103	0.250	0.093	0.143	0.117	0.086	0.120	0.359	0.221	0.294
	c	0.897	0.750	0.907	0.829	0.883	0.914	0.880	0.641	0.779	0.706
PGM	a	0.000	0.000	0.037	0.091	0.000	0.000	0.000	0.000	0.000	0.000
	b	1.000	1.000	0.852	0.742	0.967	0.942	0.000	0.953	0.985	1.000
	c	0.000	0.000	0.111	0.167	0.033	0.058	0.083	0.047	0.015	0.000
sME	a	0.000	—	0.037	—	0.000	—	—	0.016	—	0.147
	b	1.000	—	0.963	—	1.000	—	—	0.984	—	0.853
PEP-2	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.000	0.118
	b	0.966	0.860	0.889	0.894	0.883	0.813	0.860	0.813	0.871	0.824
	c	0.034	0.140	0.111	0.106	0.117	0.188	0.140	0.156	0.129	0.058
PEP-3	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.984	1.000	1.000
mGOT	a	0.017	0.100	0.111	0.091	0.017	0.034	0.125	0.109	0.044	0.059
	b	0.983	0.900	0.889	0.909	0.967	0.966	0.875	0.891	0.956	0.941
	c	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000
mIDH	a	1.000	0.885	1.000	1.000	0.983	0.948	0.900	0.938	0.912	0.853
	b	0.000	0.115	0.000	0.000	0.017	0.052	0.100	0.062	0.088	0.147
ACP	a	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.000	0.118
	b	0.069	0.058	0.019	0.000	0.117	0.074	0.100	0.063	0.015	0.118
	c	0.93	0.942	0.889	1.000	0.800	0.926	0.880	0.828	0.970	0.735
	d	0.000	0.000	0.092	0.000	0.083	0.000	0.020	0.078	0.015	0.029
ADH	a	0.000	0.000	0.000	0.000	0.033	0.000	0.080	0.062	0.059	0.147
	b	1.000	1.000	1.000	1.000	0.967	0.100	0.920	0.938	0.941	0.853
AMY-2	a	—	0.000	—	0.071	—	0.086	0.040	—	0.088	—
	b	—	1.000	—	0.929	—	0.914	0.960	—	0.912	—

*See Table 1 and Fig. 1 for full population names and locations, respectively. Monomorphic loci in both years (1990, 1993) were Hb-1, Hb-2, post-ALB-1, post-ALB-2, H-PT-1, H-PT-2, H-PT-3, LDH2, SOD-1, GDH, EST-1, EST-3, PGI, MPI, sIDH, FUM. Monomorphic loci analyzed in only one of the years included sIDH in 1990 only and PEP1 in 1993 only.

Within-population allozyme diversity in both years increased along the north-to-south gradient of the Mediterranean ecotone. It was lowest in the northernmost populations (RG90 and RD93) and generally increased toward populations located at the southern margins of the continuous range in the northern Negev and Negev highlands (Table 4). Number of alleles per locus (A) averaged 1.4 in northern populations (RG90, RD93, BG90, and BG93) and 1.5–1.6 in southern populations (NV93,

SB90, SB93, and EZ90). Percent polymorphic loci (P) was below 31.5% in northern populations and ranged from 37.5 to 43.8% in southern populations. Expected heterozygosity (H_e) was 0.061–0.088 in the north and 0.090–0.123 in the south (Table 4). Genetic diversity did not correlate with population sample size except when low polymorphism and observed heterozygosity corresponded to the small sample ($n = 17$) at EZ90 (yet mean number of alleles per locus and Hardy-Weinberg ex-

Table 3. List of polymorphic loci and estimate of total allelic diversity (H_T) in populations of Chukar Partridges sampled in 1990 and 1993 in Israel.

Polymorphic loci	H_T 1990	H_T 1993
CK	0.16	0.16
ALB	0.01	0.01
LDH-1	0.04	0.01
sGOT	0.35	0.43
SOD-2	0.46	0.45
EST-2	0.73	0.74
sMDH	0.01	0.00
6PGD	0.31	0.28
PGM	0.09	0.15
PEP-2	0.22	0.24
PEP-3	0.01	0.00
mGOT	0.12	0.14
mIDH	0.09	0.13
ACP	0.29	0.11
ADH	0.09	0.05

pected heterozygosity were high for that sample (Table 4). We therefore performed correlation analyses for 1990 samples with and without EZ90.

The Spearman rank correlation between location ranks and expected heterozygosity estimates was significant ($p < 0.05$) in both years (Table 5) and in 1993 was significant also for observed heterozygosity, percentage of polymorphic loci, and mean number of alleles per locus. The Spearman rank correlation between location and percent polymorphic loci was also significant ($p < 0.001$) in 1990 populations when EZ90 was omitted.

Northern populations were in Hardy-Weinberg equilibrium at most polymorphic loci, except for RD93, which had three loci not in equilibrium. By contrast, five loci in

Table 4. Estimates of allelic diversity in populations of Chukar Partridges sampled in 1990 and 1993 in Israel.^a

Location	n	A	P ^b	H _o	H _e ^c
1990					
RG90	29	1.4	28.1	0.059	0.061
BG90	27	1.4	31.3	0.089	0.088
YT90	30	1.6	40.6	0.086	0.091
SB90	32	1.6	43.8	0.094	0.108
EZ90	17	1.6	37.5	0.079	0.123
1993					
RD93	26	1.4	28.1	0.062	0.082
BG93	35	1.4	28.1	0.078	0.084
YT93	29	1.5	37.5	0.090	0.090
NV93	25	1.5	37.5	0.094	0.101
SB93	34	1.6	40.6	0.104	0.101

^an, mean sample size per locus; A, mean number of alleles per locus; P, percentage of polymorphic loci; H_o, mean observed heterozygosity; H_e, mean expected heterozygosity. Populations are listed from north to south (see Table 1 and Fig. 1 for details on populations).

^bA locus is considered polymorphic when more than one allele is detected.

^cUnbiased estimate based on Hardy-Weinberg equilibrium.

Table 5. Spearman rank correlation coefficients and two-tailed significance values between Israeli Chukar Partridge population rankings from north to south and diversity estimates based on 32 loci for 1990 (including EZ90) and 1993.

Genetic diversity estimate	1990 (p)	1993 (p)
Percentage polymorphic loci (P)	0.70 (0.188)	0.95 (0.014)
Observed heterozygosity (H _o)	0.30 (0.624)	1.00 (<0.001)
Hardy-Weinberg expected heterozygosity (H _e)	1.00 (<0.001)	0.97 (0.005)
Mean number of alleles per locus (A)	0.87 (0.058)	0.95 (0.014)

each of the populations SB93 and EZ90 were not in equilibrium. With the exceptions of sGOT in populations BG90 and SB93 and SOD-2 in population YT93, all departures from Hardy-Weinberg equilibrium were due to fewer than expected heterozygotes. The F_{IS} values were thereby significantly larger than 0, especially at SB90 and EZ90 in the south. A global Hardy-Weinberg equilibrium test across all loci indicated that only three populations were not in equilibrium: RD93 ($\chi^2 = 39.6$; $p = 0.0024$), SB90 ($\chi^2 = 43.7$, $p = 0.0039$), and EZ90 ($\chi^2 = 45.4$, $p = 0.001$).

Genetic Structure of Populations

Allele frequencies were heterogeneously distributed among populations in 1990 and 1993. The Φ (F_{ST}) values were 0.023 (SD = 0.009; 95% confidence interval 0.012–0.043; $p = 0.0001$) in 1990 and 0.032 (SD = 0.011; 95% confidence interval 0.008–0.046; $p = 0.0001$) in 1993. The F_{ST} values were significantly greater than 0, and about 2–4% of total genetic diversity was distributed among populations.

Estimates of gene flow (Nm), computed with Φ as an estimate of F_{ST} , suggest that, on average, 8 and 10 birds migrated among populations per generation for 1990 and 1993 samples, respectively. Lower estimates of gene flow (2 and 7 migrants per generation on average for 1990 and 1993, respectively) were based on the occurrence of private alleles in the populations. Differences between the two methods are expected because Φ addresses polymorphic loci shared among populations, whereas Slatkin's methods use rare alleles, which are present in only some of the populations. Similar differences were noticed in previous studies (e.g., Larson et al. 1984). These Nm values suggest consistent gene flow among populations. The Nm values >1 indicate that populations are panmictic, at least in conditions of genetic equilibrium (Varvio et al. 1986).

Isolation by distance was detected in both years (Fig. 2a & 2b). Regression coefficients (with $\log(\hat{M})$ estimated with Φ) were $b = -0.614$ (1990) and -0.506 (1993). The Mantel test revealed highly significant negative cor-

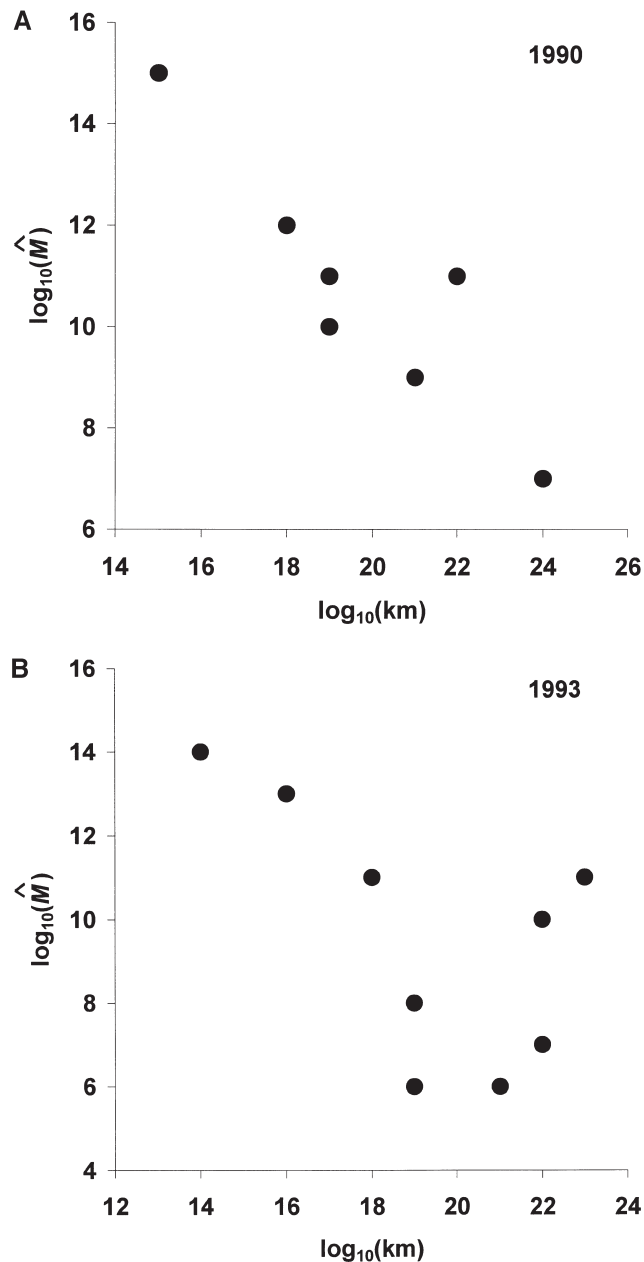


Figure 2. Relation between $\log_{10}(\hat{M})$ estimated with Φ and $\log_{10}(\text{distance in km})$ among pairwise Israeli Chukar Partridge populations sampled in 1990 and 1993. There are 10 pairwise distance values for each of the 2 years. Double points sharing x, y coordinates are the three points with $\log_{10}(\hat{M}) \leq 10$ in Fig. 2a, and the point $\log_{10}(\hat{M}) = 6$ and $\log_{10}(\text{km}) = 19$ in Fig. 2b. Parameters of the linear regressions are $a = 2.224$, $b = -0.614$ for 1990 and $a = 1.906$, $b = -0.506$ for 1993. Spearman rank correlation coefficients were significant ($p < 0.001$).

relations between geographical distance and gene flow among populations (Fig. 2).

Average linkage disequilibrium (R) values in both years were generally lower in northern than southern popula-

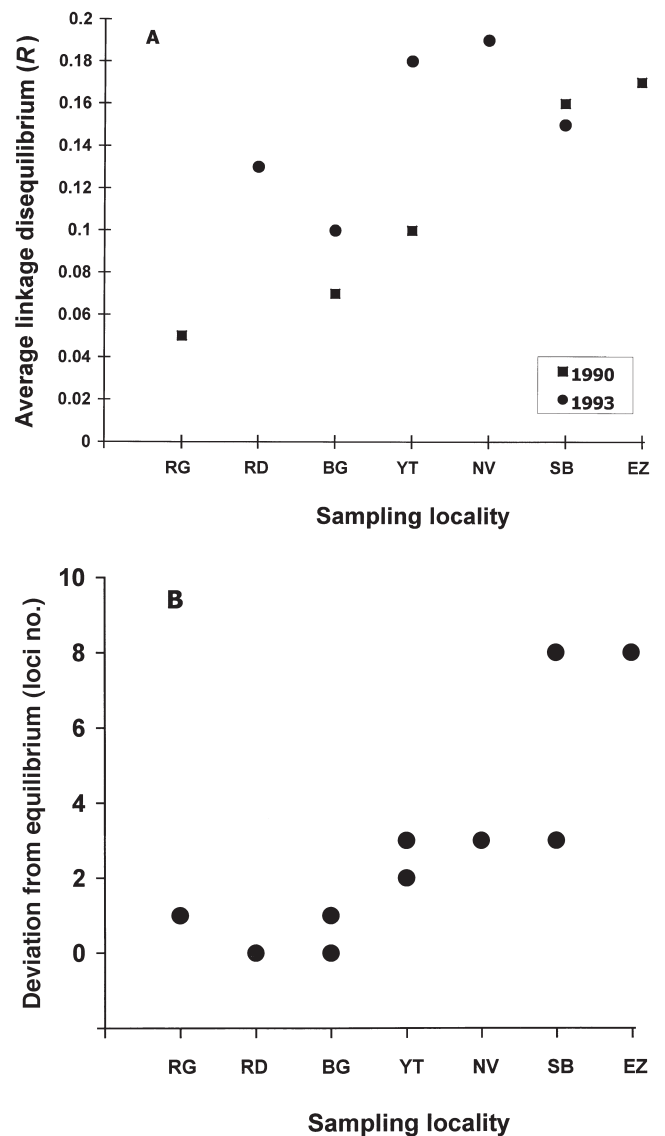


Figure 3. Average linkage disequilibrium (R) along the north-south cline of study sites in Israel (a) and number of loci with significant deviation from Hardy-Weinberg equilibrium (b). See Table 1 for key to population codes. Sampling localities appear from north to south.

tions (Fig. 3a) and were significantly correlated with location ordinal ranking in 1990 ($p < 0.0001$, Spearman rank correlation). The number of pairs of loci with significant linkage disequilibrium in each population increased toward more southern populations (Fig. 3b).

Discussion

Spatial Trends in Diversity and Evolutionary Mechanisms

Genetic diversity differed significantly among chukar populations separated by relatively short geographical

distances but subjected to a steep environmental gradient within the species' continuous range in Israel. Allelic diversity and heterozygosity increased from northern to more southern populations and were most pronounced around the transition zone of Mediterranean, desert, and steppe biomes in the northern and central Negev. Our findings support the hypothesis that high within-population genetic diversity is associated with ecotones. Genetic diversity correlated significantly with location along a gradient moving from the Mediterranean regions toward the ecotone for percentage of polymorphic loci, for observed and expected heterozygosity, for average number of alleles in 1993, and for expected heterozygosity in 1990. Increased intrapopulation genetic diversity in the ecotone region resulted from the addition of new alleles not present in less variable populations and from the increasing frequency of rare alleles at polymorphic loci.

Departures from Hardy-Weinberg equilibrium were usually low, with the exception of the southernmost populations (SB90, SB93, and EZ90). Linkage disequilibria increased toward the south, where a significant deficiency of heterozygotes was found. Populations sampled in northern and central Negev were the most variable and showed the highest values of intra- and interlocus genetic disequilibria. Both 1990 and 1993 populations showed instances of isolation by distance effects in the face of both short distances between populations and the absence of significant geographical barriers. These trends were evident even though both years' data indicated the likelihood of substantial gene flow among populations.

A heterogeneous geographical distribution of genetic diversity among chukars in Israel corresponds somewhat with evidence of geographical differences in chukar morphology (e.g., size and plumage; Randi & Alkon 1994). Two subspecies of chukar (*A. c. cypriotes* and *A. c. sinaica*) are currently recognized in the region (Watson 1962; Cramp & Simmons 1980; Shirihai 1996), although the patterns of variability of diagnostic morphological traits across their putative contact zone have not been studied carefully. This raises the question of whether the high ecotone diversity can be related to recontact of formerly isolated populations following the Quaternary glacials (Yom-Tov & Tchernov 1988). Yet earlier morphological studies (Nissani 1974) and available paleontological findings (Yom-Tov & Tchernov 1988) suggest that clearly distinct *A. c. sinaica* occur only in the southern Sinai desert and that the extant isolated population in the Sinai Mountains is a post-glacial relict (Tchernov 1988) from the Upper Pleistocene glacials. Distribution of chukars during those periods was mostly continuous throughout the southern parts of Israel and Sinai, including currently more arid areas where chukars are not present or are rare (Shirihai 1996; E. Tchernov, personal communication). Thus, all seven Israeli populations we examined compose a single subspecies, *A. c. cypri-*

otes, and the argument for the historical recontact of chukar populations in the Mediterranean-desert ecotone causing increased diversity does not seem convincing.

We do not know the genetic basis of morphological divergence and physiological adaptations of chukars to various environmental conditions and we are not aware of links among allozyme variants and genes controlling quantitative traits in chukars. Allozyme variants usually are not selected directly and can often be treated effectively as neutral genes in population and phylogenetic studies (Skibinski et al. 1993). They may be linked, however, to adaptive and strongly selected genes and thereby subject to temporary selection via "hitchhiking" (Pemberton et al. 1988; Bancroft et al. 1995). The unique and highly variable genetic structure of ecotonal chukar populations could thereby be maintained by a combination of isolation by distance through reduced gene flow and natural selection acting on morphophysiological traits and on their linked allozyme loci.

Wright's (1943) isolation-by-distance model predicts reduced heterozygosity in local demes and increasing allelic divergence with increasing distance between demes. Such geographic structuring can mimic the genetic effects of selection in heterogeneous habitats, although it can also be generated by dispersal and random drift (Ender 1977). In terms of Wright's F statistics (Wright 1965), isolation by distance will produce values of F_{IS} and F_{ST} significantly greater than 0, but Hardy-Weinberg and linkage disequilibria are not predicted by the theory. The chukar populations exhibited isolation by distance, coupled with increasing allelic diversity, and Hardy-Weinberg and linkage disequilibria along the gradient. Heterozygote deficit and linkage disequilibria can be generated by frequent population turnovers, such as elevated rates of local extinction and recolonization among populations, possibly associated with natural selection against recombinant genomes resulting from mating among individuals from genetically divergent populations (Barton & Hewitt 1989). Significant F_{IS} values combined with increased linkage disequilibrium in populations at the margins of the chukar's continuous range suggest that it may face selective pressures.

Thus, a simple isolation-by-distance model does not suffice to explain our findings. At this stage, we cannot discriminate between historical and actual rates of gene flow, and we do not know the actual dispersal rates for Israeli chukar populations. Although Nm , as estimated by F_{ST} , relies on polymorphisms shared among populations and may represent a persistent genetic population structure, Nm estimated with private alleles should be more tightly linked to the occurrence of recent mutations in every population. Actual rates of gene flow could thereby be much smaller than historical ones. Indeed, we found that Nm , estimated with private alleles, was 2 and 7 for the 2 years of study, as compared with 8 and 10 based on F_{ST} .

Conservation

Although the causes of the observed genetic diversity trends in chukars along an environmental ecological gradient in Israel are presently unclear, recognition of a spatial trend can facilitate conservation planning and the identification of populations and areas that may warrant special attention (Safriel et al. 1994; Lomolino & Channell 1995). Genetic diversity within natural populations along this gradient shows significant trends and is not uniform. This is in spite of the steepness of the ecological gradient and hence the short distances between the study populations of this species.

Several conservation recommendations can be derived: Northern Negev chukar populations within the ecotone area should receive high conservation priority because they may guarantee the maintenance of high within-species diversity. These ecotone populations may function as sources of genetic variability for other populations, some of which may be sink populations (Pulliam 1988; Dias 1996; Hanski & Simberloff 1997) whose persistence may depend on dispersing individuals and genotypes originating from these regions. Management should ensure that dynamic populations and adaptive processes (Lacy 1997) in ecotone populations be maintained. Conservation priority should also be given to populations along the gradient in Israel from the northern Mediterranean region toward the ecotone. Populations along this gradient not only contain increasing levels of diversity in general but have unique alleles as well as most alleles present in other populations.

Conservation of chukar populations and metapopulation processes must contend with the continued development and rapid urbanization of wide areas in Israel. Habitat fragmentation appears especially severe in the densely populated areas of northern and central Israel. Even the ecotone area of the northern Negev is rapidly being developed and fragmented, with an ever-diminishing likelihood of gene flow among local populations. Therefore, an important management priority may be to create or identify existing habitat corridors that are essential links among chukar populations. Enabling connection between suitable habitat areas in the face of fragmentation may be required for conserving connectivity, gene flow, and diversity within populations and preventing the genetic and demographic stochastic processes that lead to loss of diversity and local population extinction (Thomas & Hanski 1997). Landscape-level assessments (Wiens 1997) and monitoring are necessary first steps in preventing isolation of local chukar populations and conserving essential links among them.

A different landscape dynamic applies to and is changing patterns of distribution (Shirihai 1996) in areas of the central and southern Negev desert, where irrigation-based agriculture and settlement are creating rich habitat patches in areas that formerly supported only sparse

chukar populations. Populations SB90, SB93, and EZ90 are located in relatively small, recently established local "islands" of orchards and agricultural fields within a surrounding arid environment (mean annual rainfall approximately 100 mm; Israel Meteorological Service) in which chukar density is lower. Because of this, we include them here as part of the ecotone and not as true desert populations. We are currently comparing the genetic characteristics of desert chukar populations in natural and neighboring irrigated agricultural environments. We hypothesize that these recent changes may have already affected patterns of dispersal and genetic diversity. Increased gene flow to the unnaturally rich patches may bring uniformity to allele frequencies among local populations (Mills & Allendorf 1996).

In this framework, maintaining a delicate balance between reduced rates of gene flow, which may result in the deterioration of diversity in local populations, and increased gene flow, which may result in uniformity of allele frequencies between local populations and may prevent populations from responding to local selection pressures, is essential for the preservation of the genetic structuring along the gradient and maintenance of the unique genetic attributes of local populations (Mills & Allendorf 1996).

Our findings have revealed a substantial measure of genetic structuring among Israeli chukar populations and suggest that the genetic structure of populations along the gradient may depend on a fine balance between isolation from and connectivity with neighboring populations (Mills & Allendorf 1996). Accordingly, the increasing human-induced changes to the environment and to the rates of gene flow among populations should be counteracted so as to restore this balance.

Chukars have large, natural Eurasian distributions and were successfully introduced to North America, New Zealand, and elsewhere (Cramp & Simmons 1980; Shirihai 1996). Although the species has not acquired threatened status at the global level, it is likely that local vulnerable populations exist within the species' range, mainly due to habitat loss and hunting, that may warrant special attention. We suggest that ecotone populations in Israel comprise such a unique genetic resource. Future efforts to restore chukars to their former ranges may depend on identifying and preserving areas with extant populations rich in genetic diversity.

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